Effects of correlated Gaussian noise on the mean firing rate and correlations of an electrically coupled neuronal network

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In this paper, we examine the effects of correlated Gaussian noise on a two-dimensional neuronal network that is locally modeled by the Rulkov map. More precisely, we study the effects of the noise correlation on the variations of the mean firing rate and the correlations among neurons versus the noise intensity. Via numerical simulations, we show that the mean firing rate can always be optimized at an intermediate noise intensity, irrespective of the noise correlation. On the other hand, variations of the population coherence with respect to the noise intensity are strongly influenced by the ratio between local and global Gaussian noisy inputs. Biological implications of our findings are also discussed.

It is thoroughly documented and established that noise can play a constructive role in neuronal systems. Noise correlations, which have been observed in the brain, are thereby usually assumed to be ignorable. However, it has been shown that noise correlations cannot be avoided and may indeed play a vital role in neuronal dynamics, mainly because they affect the amount of information transmitted across the cortex as well as the computational strategies of neuronal networks. In the context of transmission of neuronal information, there is an ongoing debate about whether a cortical neuron is sensitive to the mean firing rate of presynaptic neurons and their correlations or not. Regardless of this, the mean firing rate and the correlations among neuronal groups are two important factors determining the transmission of information across the network. Here we elaborate on the effects of correlated Gaussian noise (noise correlation) on the mean firing rate and the correlations among neurons of an electrically coupled neuronal network. We find that the noise correlation has little effect on the variations of the mean firing rate with respect to the noise intensity. Variations of the population coherence with respect to the noise intensity, however, are strongly influenced by the ratio between local and global Gaussian noise in the overall noise intensity, which can be tuned by the noise correlation. Our results indicate that noise correlation may have a significant impact on the response of postsynaptic neurons if these are sensitive to correlated neuronal activities.

I. INTRODUCTION

Neurons are usually subject to random fluctuations on different scales, ranging from channel noise created by random ion flow across the plasma membrane to synaptic noise created by the activity of other neurons. In experiments, it has been shown that noise has constructive effects on neuronal dynamics. For example, William and Durand[1] showed that an appropriate noise intensity can improve the detection of subthreshold signals in a resonant manner. Higgs et al.[2] found that synaptic noise increases the gain in many pyramidal neurons with large sAHP (slow after hyperpolarization). Jacobson et al.[3] found that channel noise contributes significantly to membrane voltage fluctuations at the subthreshold voltage range. In theoretical and computational studies, the constructive role of noise in neuronal systems has been reported as well. For example, it was shown that noise is able to evoke coherence and stochastic resonance in single neurons,[4–8] as well as in one-dimensional[9,10] and two-dimensional[11–14] neuronal networks. Related to the present study, in the sense that correlated noisy inputs have been considered, are the two papers by Kreuz et al.[7,8] where it has been shown that an intermediate noise intensity can evoke the most coherent temporal output of a single neuron irrespective of the noise correlation length. Double coherence resonance in terms of an optimal combination of noise intensity and correlation was reported as well. Notably, the effect of auto- and cross-correlations of input spikes on the response of spiking neurons has also been studied extensively.[15] Additionally, noise can also induce

and/or enhance the synchronization in neuronal systems.[10,16] Refs. 17 and 18 are two comprehensive review papers, recommended to the readers who are interested in the research of noise effects on nonlinear systems in general, including neuronal dynamics.

In the cortex, a single interneuron can be connected with tens of thousands of local circuit interneurons. Thus, activity of this single interneuron will provide correlated input to many neurons in the local circuit.[19] Furthermore, correlated inputs might be stimulus driven and usually are random. These random correlated inputs can be described by means of correlated noise. In the past, noise correlations have, apart from a few exceptions,[7,8] usually been ignored. But some researchers have found that noise correlations can have many different effects on the neuronal population − the amount of information encoded, the computational strategies of networks of neurons, etc., as reviewed in Ref. 20. This means that noise correlations should not be neglected in neuronal systems. Adding to this conclusion is also the fact that the conceptually related coupling via noise in one-dimensional[21] and two-dimensional[22] systems has been found to induce synchronization. Meanwhile, the question of how a postsynaptic neuron is affected by the presynaptic neuronal population is still not fully understood. There is an ongoing debate on whether a cortical neuron is driven mainly by the mean firing rate of presynaptic neurons or by correlated firing activities.[23–25] No matter what the outcome of the debate, the mean firing rate and correlations of neuronal groups are two important factors in investigating transmission of neuronal information. Therefore, we will investigate the effects of correlated Gaussian noise (noise correlation) on the mean firing rate and correlations of a neuronal population in this paper. The obtained results may have important implications for understanding the transmission of neuronal information.

The paper is organized as follows. Equations governing the two-dimensional neuronal network are presented in the next section. Measures used for quantifying the observed neuronal dynamics are introduced in section III, while the results due to correlated Gaussian noise are presented in section IV. Finally, the summary is given in section V. We also provide an algorithmic description of noise generation in the Appendix.

II. EQUATIONS OF THE NETWORK

The Rulkov map[26,27] is employed to model the dynamical behavior of neurons constituting the examined neuronal network. The model captures succinctly main dynamical mechanisms in real neuronal ensembles, foremost showing typical restructuring of collective behavior following stochastic inputs. Specifically, we consider a network of $N \times N$ electrically coupled Rulkov maps

$$
\begin{aligned}
u_{n+1}(i,j) = &\, \alpha/[1 + u_n^2(i,j)] + v_n(i,j) + D[u_n(i+1,j) \\
&+ u_n(i-1,j) + u_n(i,j-1) + u_n(i,j+1) \\
&- 4u_n(i,j)] + \eta_n(i,j), \\
v_{n+1}(i,j) = &\, v_n(i,j) - \beta u_n(i,j) - \gamma,
\end{aligned}
$$

where $u_n(i,j)$ is the membrane potential of neuron (i,j) and $v_n(i,j)$ is the corresponding ion concentration at the discrete time n. The system parameters are α, β and γ, whereby the latter two determine the time scale associated with the dynamics of the slow variable $v_n(i,j)$ and α is the main bifurcation parameter. If not stated otherwise, we use $\alpha = 1.99$ and $\beta = \gamma = 0.001$, for which each neuron is governed by a single excitable steady state $(u^*, v^*) = (-1, -1 - \alpha/2)$. Each neuron is coupled electrically with its four nearest neighbors with periodic boundary conditions given by $u(0,j) = u(N,j), u(N+1,j) = u(1,j), u(i,0) = u(i,N), u(i,N+1) = u(i,1)$. Finally, D is the coupling strength between the neurons on the 128×128 spatial grid.

The correlated Gaussian noise $\eta_n(i,j)$ is expressed as

$$
\eta_n(i,j) = \sqrt{R}e_n + \sqrt{1-R}\xi_n(i,j), \tag{1}
$$

where e_n is the Gaussian white noise and common to all units, *i.e.* global noise, with the properties:

$$
\begin{cases}
\langle e_n \rangle = 0, \\
\langle e_n e_m \rangle = 2\sigma \delta_{m,n},
\end{cases} \tag{2}
$$

and $\xi_n(i,j)$ is the local Gaussian noise, which is uncorrelated from site to site. $\xi_n(i,j)$ is taken as Gaussian white noise with the properties:

$$
\begin{cases}
\langle \xi_n(i,j) \rangle = 0, \\
\langle \xi_n(i,j)\xi_m(i',j') \rangle = 2\sigma_{loc}\delta_{i,i'}\delta_{j,j'}\delta_{m,n},
\end{cases} \tag{3}
$$

and Gaussian colored noise with the properties:

$$
\begin{cases}
\langle \xi_n(i,j) \rangle = 0, \\
\langle \xi_n(i,j)\xi_m(i',j') \rangle = \sigma_{loc}\lambda exp(-\lambda|n-m|)\delta_{i,i'}\delta_{j,j'},
\end{cases} \tag{4}
$$

respectively. Here σ is the noise intensity of the global noise e_n, σ_{loc} is the noise intensity of the local noise $\xi_n(i,j)$, and λ^{-1} is the correlation time of the local Gaussian colored noise. Here we set $\sigma_{loc} = \sigma$ and $\lambda = 0.05$. The parameter R measures the noise correlation between a pair of neurons. $\eta_n(i,j)$ is renewed at each iteration step n and for each unit (i,j) in the iterated processing according to the algorithm proposed in Ref. 28 (see Appendix for details). In the following discussions, we will take σ and R as controlled parameters.

III. MEASURES OF NEURONAL DYNAMICS

Two measures for quantifying the observed neuronal dynamics due to the impact of noise are employed. One is the mean firing rate Π,[29] and the other is the population coherence κ.[30,31] The mean firing rate of the neuronal network is defined as

$$
\Pi = \langle \pi(n) \rangle_T = \left\langle \frac{1}{N^2}\sum_{ij}\theta[u_n(i,j) - u_{th}] \right\rangle_T, \tag{5}
$$

where $u_{th} = -0.2$ is the firing threshold determined by the action potential of the Rulkov neuron. Notably, $\theta(x)$ is a heaviside function with $\theta(x) = 1$ if $x \geq 0$ and $\theta = 0$ if $x < 0$. The

bracket $\langle \rangle$ indicates the average over the whole iteration time T.

To quantify the correlations of firing events in the neuronal network, we introduce the population coherence measure $\kappa(\tau)$.[30,31] $\kappa(\tau)$ is defined as the average of the local coherence $\kappa_{ij}(\tau)$ over all the pairs of neurons, namely:

$$\kappa(\tau) = \frac{1}{C_N^2} \sum_{i,j=1;i\neq j}^{N} \kappa_{ij}(\tau) = \frac{1}{\frac{N(N-1)}{2}} \sum_{i,j=1;i\neq j}^{N} \kappa_{ij}(\tau),$$

(6)

where

$$\kappa_{ij}(\tau) = \frac{\sum_{l=1}^{m} Y_i(l)Y_j(l)}{\sqrt{\sum_{l=1}^{m} Y_i(l) \sum_{l=1}^{m} Y_j(l)}}.$$

(7)

The coherence $\kappa_{ij}(\tau)$ between any two neurons i and j is measured by the cross-correlation of their spike trains at zero time lag within a time interval τ. More specifically, we divide the full iteration time T into small bins of duration $\tau = 70$ and define the two spike trains as $Y_i(l) = 0$ or 1 and $Y_j(l) = 0$ or 1 ($l = 1, 2, ..., m; T/m = \tau$), whereby $Y(l) = 1$ if the onset of a spike occurred at the l-th time bin, otherwise $Y(l) = 0$. Sometimes, the population coherence measure $\kappa(\tau)$ is also used to quantify the synchronization of neuronal firings in networks.[30,32] Larger population coherence κ corresponds to higher correlations between neurons inside the network.

IV. EFFECTS OF CORRELATED GAUSSIAN NOISE

In order to discern clearly the distinct effects of correlated Gaussian noise on neuronal dynamics, we consider firstly the effects of *local* Gaussian noise, i.e., $R = 0.0$. Variations of the mean firing rate Π and the population coherence measure κ with respect to the noise intensity σ for various coupling strengthes D are shown in Figs. 1 and 2. Importantly, local Gaussian noise is white in Figs. 1 but colored in Figs. 2. From these two figures, we can see that Π and κ can reach larger values at an intermediate noise intensity than at smaller and larger noise intensities, for both local Gaussian white and colored noise. We caution, however, that for large noise intensities the mean firing rate Π may yield spurious results because of the very noisy output of individual neurons forming the neuronal network, due to which it is practically impossible to discern what is a firing event and what not. In accordance with this, the results depicted in this paper are constrained to noise intensities for which the neuronal dynamics still plays a significant role, i.e., is not completely overshadowed by noise.

The above-reported results can be interpreted as follows. Small noise intensities are unable to evoke excitations, accordingly, the mean firing rate Π becomes zero and the coherence of neurons inside the network is small (*i.e.* κ is small). For intermediate noise intensities, typically only a few neurons (at random) forming the lattice start firing. Due to the diffusive

coupling and the noisy support the excitations can propagate regularly to the neighbors, which results in well ordered circular waves (as shown in Ref. 13) that ultimately result in high firing rate Π and large coherence κ. While for large noise intensities, neurons inside the network exhibit high-rate spiking behavior. When such spiking neurons are coupled diffusively, they tend to suppress the inputs coming from other neurons, which in turn decreases the number of firing events in a time span and destroys the spatial order of the dynamics, finally leading to small Π and a decreases of κ. Therefore, for local Gaussian noise, the mean firing rate and the correlations of the neuronal network can be optimized by some intermediate noise intensities, as shown in Figs.1 and 2.

In what follows, we examine more closely the effects of correlated Gaussian noise via controlling the noise correlation R. Variations of the mean firing rate Π and the population coherence measure κ with respect to the noise intensity σ for various noise correlations R are shown in Figs.3 and 4. The local Gaussian noise is taken as white in Figs.3 and colored in Figs.4, respectively. Compared with the results shown in Figs.1(a) and 2(a), we can see that variations of Π with respect to the noise intensity σ under correlated Gaussian noise are similar as the ones under local Gaussian noise.

For the population coherence κ, however, we can see that its variations versus the noise intensity σ are strongly dependent on the noise correlation R as shown in Figs.3(b) and 4(b). It is also worth pointing out that the occasional non-smoothness of the curves in the later two figures is predominantly a consequences of the somewhat erratic switching between the emergence of spatially ordered patterns and their absence on the network. The latter introduces some non-smoothness to the employed statistical quantifiers, yet we found it impossible to eliminate this by means of more intensive numerical investigations. The reader is also referred to Ref. 13, where pattern formation due to correlated Gaussian noise has been studied earlier. Through comparisons with the corresponding results presented in Figs. 1(b) and 2(b), we find that effects of correlated Gaussian noise on the population coherence κ look more complex than the ones of local Gaussian noise. In the case of local Gaussian white noise, as shown in Fig. 3(b), a weak coherent behavior (there exists a small peak at an intermediate σ) can be observed for small R, e.g., $R = 0.1, 0.3$. And for an intermediate R ($R = 0.5, 0.7$), the variations of κ become irregular with changing of the noise intensity. With further increasing of R, a plateau region of κ emerges as the noise intensity σ increases, as can be observed from the line corresponding to $R = 0.9$, for example. For local Gaussian colored noise, variations of κ with respect to σ are irregular at $R = 0.1$, and exhibit plateau regions with increasing of σ for large R, as presented in Fig. 4(b).

Notably, the underlining mechanism regarding the effects of correlated Gaussian noise on the mean firing rate Π is similar as discussed above in the case of local Gaussian noise. However, in order to clarify the effects of noise correlation R on the complicated variations of κ versus σ, we introduce the quantity

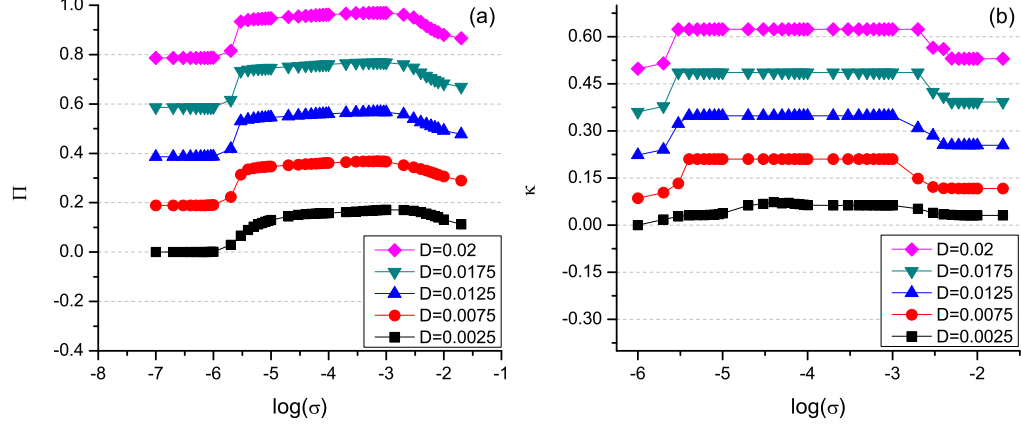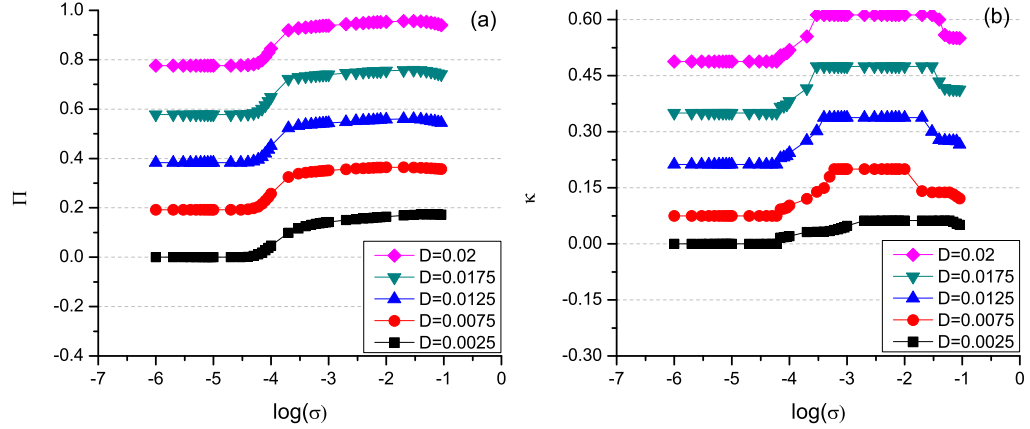$$\rho = \frac{2R\sigma}{(1-R)\langle \xi(i,j) \rangle^2},$$

(8)

FIG. 1: Stack lines by Y offsets of the mean firing rate Π (a) and the population coherence measure κ (b) in dependence on the noise intensity σ of additive local (we set $R = 0.0$) Gaussian white noise for various coupling strength D. Note that the x-axis has a logarithmic scale.

FIG. 2: Stack lines by Y offsets of the mean firing rate Π (a) and the population coherence measure κ (b) in dependence on the noise intensity σ of additive local (we set $R = 0.0$) Gaussian colored noise for various coupling strength D. Note that the x-axis has a logarithmic scale.

which is the noise strength ratio between global and local noise. $\rho = R/(1 - R)$ when local noise is taken as Gaussian white noise, and $\rho = 2R/(1 - R)\lambda$ when it is taken as Gaussian colored noise. Thus, values of ρ can be controlled by the noise correlation R and λ. We calculate the variations of κ with respect to σ for different noise intensity ratios ρ, or equivalently, different pairs of (R, λ). The obtained results are presented in Fig. 5(a), where pairs of R and λ are colored black if the variation of κ with respect to σ shows a weak coherence. At this point it is instructive to examine the corresponding curves for $R = 0.1$ and 0.3 that are depicted in Fig. 3(b). Conversely, pairs of R and λ are colored gray if variations of κ with respect to σ are irregular, as can be observed observed from the corresponding curves for $R = 0.5$ and 0.7 in Fig. 3(b) and from the curve depicted for $R = 0.1$ in Fig. 4(b). Finally, (R, λ) pairs are colored white if there exists a plateau region of κ for large σ, as can be observed in

Fig. 3(b) for $R = 0.9$ and in Fig. 4(b) for $R = 0.3$, 0.5, 0.7 and 0.9. In order to now appreciate the quantity ρ introduced in Eq. (8) as an important driving force behind the variations κ with respect to σ, we show in Fig. 5(b) how ρ varies for different pairs of R and λ in a systematic manner. In particular, from thus far presented results it can be concluded that there exist three intervals of ρ, i.e. $(0, a)$, $[a, b)$, $[b, \infty)$, within which the variations of κ with respect to σ are different from one another. In Fig. 5(b) black is used for those combinations of R and λ for which $0.0 < \rho < 2.0$, gray is used if $2.0 \leq \rho < 8.0$, while white is used if $8.0 \leq \rho < \infty$. Compared to results presented in Fig. 5(a), we can observe at a glance that by setting a and b to equal 2.0 and 8.0, respectively, the color patterns match nearly perfectly, from which we conclude that ρ indeed has a decisive impact on variations of κ with respect to σ.

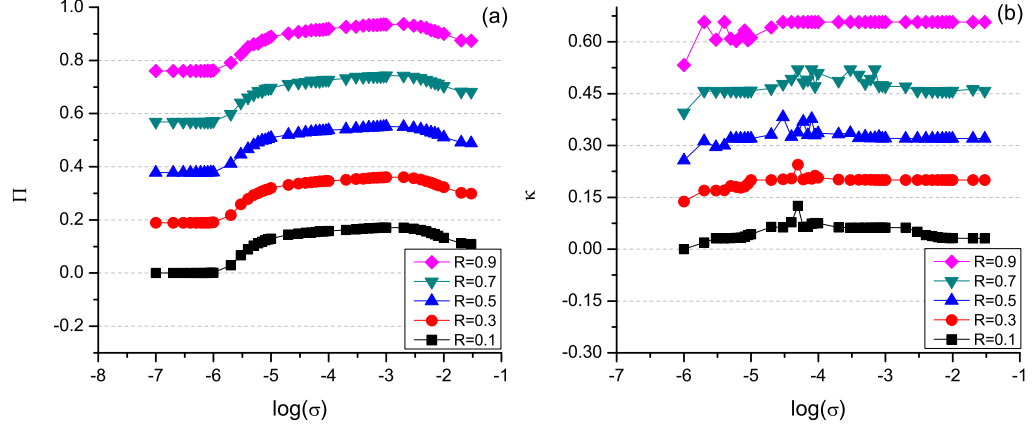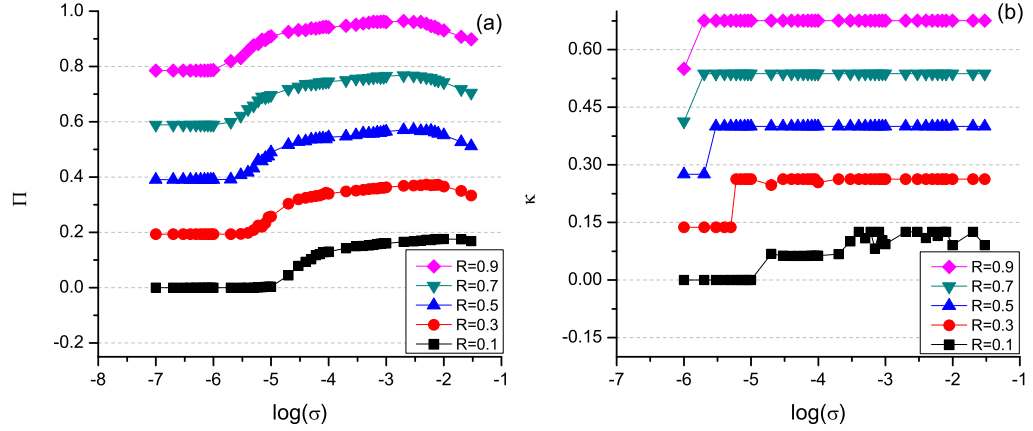From the analysis of the effects of correlated Gaussian

FIG. 3: Stack lines by Y offsets of the mean firing rate Π (a) and the population coherence measure κ (b) in dependence on the noise intensity σ of additive correlated global noise $\eta(i,j)$ with local Gaussian white noise for various noise correlations R. The coupling strength is constant, equalling $D = 0.0025$. Note that the x-axis has a logarithmic scale.

FIG. 4: Stack lines by Y offsets of the mean firing rate Π (a) and the population coherence measure κ (b) in dependence on the noise intensity σ of additive correlated global noise $\eta(i,j)$ with local Gaussian colored noise for various noise correlations R. The coupling strength is constant, equalling $D = 0.0025$. Note that the x-axis has a logarithmic scale.

noise, we now thus know that noise correlations have no notable effects on the variations of Π versus σ, while conversely, the noise correlation R plays a crucial role in how κ varies with respect to σ, in particular by means of controlling the noise strength ratio ρ.

V. SUMMARY

In this paper, we have studied effects of correlated Gaussian noise on neuronal firings, measured by the mean firing rate and the population coherence, of a two-dimensional network, which is locally modeled by the Rulkov map. Based on our numerical simulations, we have found that the mean firing rate of the network Π can be enhanced at some intermediate noise intensities by correlated Gaussian noise for any noise correlation R. This phenomenon is similar as the coherence resonance, even though there is not a well-defined optimal noise intensity. While for population coherence measure κ, we find that its variations with respect to noise intensity are very complex. Furthermore, we reveal that it strongly depends on the ratio ρ. Moreover, through the measure for population coherence κ, we have been able to gain a deeper understanding of the interactions between global and local noise. In particular, we have shown that an appropriately tuned global noise can be an effective promotor of correlations of firing events in the neuronal network.

As we have already stated in the Introduction, it is still debatable whether a cortical neuron is driven mainly by the mean firing rate of presynaptic neurons or by correlations between
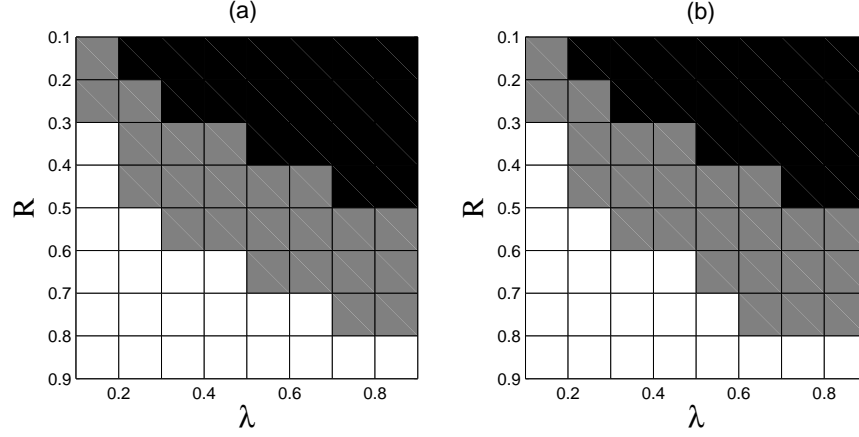
FIG. 5: (a) Variations of κ with respect to σ for different (R, λ) pairs. If the coherence of κ with respect to σ is weak then the corresponding (R, λ) pairs are colored black. If the variations of κ with respect to σ are irregular the color is gray, while it is white if there exists a plateau region of κ for large σ. (b) The dependence of ρ on different (R, λ) pairs. Color black is used for those combinations of R and λ for which $0.0 < \rho < 2.0$, gray is used if $2.0 \leq \rho < 8.0$, while white is used if $8.0 \leq \rho < \infty$. See also the main text for further details.

pairs of neurons inside the neuronal network. Moreover, neurons inside neuronal networks are not only affected by local random fluctuations, but also stimulated by some common random inputs. Thus, the results obtained for discussing effects of correlated Gaussian noise on the mean firing rate and correlations of the neuronal network may give some important implications on investigating transmission of neuronal information in neuronal networks.

Appendix: Noise generation

Gaussian white noise e_n can be generated effectively for map-based neuronal networks as follows. Let

$$
\begin{aligned}
a &= \text{random number}, \\
b &= \text{random number}, \\
e_n &= [-4\sigma \ln(a)]^{1/2} \cos(2\pi b),
\end{aligned} \tag{A.1}
$$

where a and b are uniformly distributed on the unit interval. When $\xi_n(i, j)$ is Gaussian white noise, e_n will be renewed according to Eq. (A.1) at each iteration step n and for each unit (i, j). When $\xi_n(i, j)$ is a Gaussian colored noise, however, it can be generated by means of

$$
\begin{aligned}
a &= \text{random number}, \\
b &= \text{random number}, \\
g_w &= [-4\sigma \Delta t \ln(a)]^{1/2} \cos(2\pi b), \\
\xi_{n+1} &= \xi_n - \lambda \xi_n + \lambda g_w,
\end{aligned} \tag{A.2}
$$

with initial conditions

$$
\begin{aligned}
l &= \text{random number}, \\
m &= \text{random number}, \\
g_c &= [-4\sigma \lambda \ln(l)]^{1/2} \cos(2\pi m),
\end{aligned} \tag{A.3}
$$

where a, b, l and m are uniformly distributed on the unit interval. Subsequently, $\eta_n(i, j) = \sqrt{R} e_n + \sqrt{1 - R} \xi_n(i, j)$ is renewed at each iteration step n and for each unit (i, j) by repeating Eqs. (A.2) and (A.3).

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